

Appendix II

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Considering Biological Processes

COMMENTARY

The Importance of Considering Biological Processes when Setting Total Maximum Daily Loads (TMDL) for Phosphorus in Shallow Lakes and Reservoirs

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Abstract

Total maximum daily loads (TMDL) are required by the US Environmental Protection Agency for pollutants that have impaired the designated uses of surface waters in the nation. Setting an appropriate TMDL requires quantitative information on both the external pollutant inputs and the processes affecting pollutant dynamics within the ecosystem. Here we focus on phosphorus (P), a globally important pollutant of freshwater lakes. We consider how biological processes (including those related to algae, plants, invertebrates and fish) can influence the ability of lakes to assimilate P, and in turn the ability of managers to select appropriate TMDLs. The primary focus is on shallow eutrophic lakes, with Lake Okeechobee (Florida, USA) serving as a case study. The paper deals only with in-lake processes as they relate to setting the TMDL and not the subsequent issue of load allocation among pollution sources. The results indicate that the ability of a shallow lake to assimilate P is substantially reduced when surplus levels of P occur in the water column, the phytoplankton become dominated by cyanobacteria, the benthic invertebrate community becomes dominated by oligochaetes, and submerged plant biomass is low. If some of these biological changes can be reversed in a rehabilitation program then the lake may be able to support a higher TMDL.

Introduction

The US Clean Water Act establishes a process to facilitate recovery of surface waters not meeting their established water quality standards. In the Act, state and/or federal agencies are charged with developing an appropriate TMDL for each water body

and for each identified pollutant. Under Section 303(d)(1)(C) of the Act, a TMDL is identified as "the load necessary to implement the applicable water quality standards." In other words, it identifies the amount of pollutant loading that a water body can receive and still provide its designated uses (e.g., drinking water, recreation, fish & wildlife habitat). In the USA and other nations one of the most frequently identified pollutants of lakes and reservoirs is phosphorus (P), which can originate from urban, residential, industrial and non-point agricultural sources (Reynolds 1978, Cullen and Forsberg 1988, Havens and Steinman 1995). Because P often is limiting to phytoplankton production in freshwater lakes (Schindler 1977, Hecky and Kilham 1988), high inputs of this nutrient have led to accelerated eutrophication and in many instances to dense blooms of noxious cyanobacteria (Paerl 1988, Smith et al. 1999). Prolonged high inputs of P result in a variety of other adverse impacts to the natural ecosystem, as we shall discuss below.

Setting a TMDL for P generally requires identification of a lake water concentration standard above which the uses of the resource are considered to be impaired. Empirical relationships or models are then used to quantify the external loading rate necessary to achieve the standard. In this computation, it is necessary to consider the extent to which the ecosystem can process and assimilate P into long-term (sediment) storage. Quantifying this lake "assimilative capacity" is a challenge because it is determined by a complex function of physical, chemical, and biological processes that vary over time and space. Assimilative capacity is particularly difficult to quantify in shallow lakes where there are many different types of sediment-water interactions. Nevertheless, we can approximate the relationship between P assimilation and the TMDL using a mass-balance approach. This is patterned after the input-output models of Vollenweider (1975) and has been proposed as one method for setting a TMDL for Lake Okeechobee (Walker 2000).

For a lake or reservoir, the total mass input of P can be related to the mass output and net storage according to Equation 1. Under steady state conditions the TMDL can be determined by expressing output and storage terms as concentration times volume (equation 2) and then substituting into the equation the in-lake P concentration goal (equations 3-4). We assume here that the outflow P concentration is equal to that of the lake water.

$$M_{in} + M_{atmos} = M_{out} + M_{sed} \quad (1)$$

$$M_{in} + M_{atmos} = P_{lake} * Q_{out} + P_{lake} * A * K_{net} \quad (2)$$

$$M_{in} + M_{atmos} = P_{target} * Q_{out} + P_{target} * A * K_{net} \quad (3)$$

$$TMDL = P_{target} * Q_{out} + P_{target} * A * K_{net} \quad (4)$$

In these equations M_{in} is the P mass input (metric tons y^{-1}) from tributaries, M_{atmos} is the input from the atmosphere, M_{out} is the output to tributaries, and M_{sed} is the net loss of P to sediment storage. The term P_{lake} is the lake water P concentration ($mg\ m^{-3}$), Q_{out} is the outflow volume ($km^3\ y^{-1}$), A is lake area (km^2), and K_{net} is the net P sedimentation rate ($m\ y^{-1}$). All of the model terms can be directly measured except K_{net} , which is calculated by solving equation (2) using data from the lake's yearly budget. The M_{sed} term is rarely measured and is generally calculated by difference using equation (1).

Understanding how K_{net} has changed over time and how it is anticipated to change under reduced P loads is critical to setting the TMDL. However, the linkage between K_{net} and P loads may be complicated where biological processes produce feedback loops and non-linear responses. A wide body of research has shown that this situation is common in shallow eutrophic lakes (e.g., Scheffer 1998, Moss et al. 1997, Meijer 2000). Here we illustrate that biological processes can affect K_{net} and the TMDL using shallow Lake Okeechobee, Florida, USA, as an example. The biological factors are described in a hierarchical manner, from the base of the food web upward.

Description of the Study Site

Lake Okeechobee is a large ($\sim 1,800\ km^2$), shallow (mean depth $\sim 3\ m$) eutrophic lake located in South Florida, USA, at the center of the greater Florida Everglades ecosystem. The lake provides flood protection, water supply, recreational opportunities, wildlife habitat, and it supports productive sport and commercial fisheries. The lake has experienced high rates of P loading since at least the early 1970s, when regular data first were collected (James et al. 1995a), and in the last 30 years it has undergone accelerated eutrophication (Havens et al. 1996). The lake is designated by the USEPA as impaired by high concentrations of total P and a few other chemical constituents. Both the USEPA

and the Florida Department of Environmental Protection (FDEP) have proposed TMDLs for P in Lake Okeechobee that are aimed at meeting an in-lake concentration goal of 40 mg m^{-3} that was established previously by Florida Statutes (sections 373.451 and 373.4595).

Observed Trends in Phosphorus Assimilation

Based on the lake's P budget, there has been a dramatic decline in K_{net} , from above 3.0 m y^{-1} in the mid-1970s to below 1.0 m y^{-1} in recent years (Fig. 1A). This trend suggests that the lake has lost some of its capacity to assimilate P, perhaps due to saturation of P binding sites on lake sediment particles and/or other processes. The results of a recent study indicate that surface mud sediments contain a higher concentration (0.75 g m^{-3}) of dissolved reactive P than a decade ago (0.39 g m^{-3}), reflecting the effects of increased P loading and supporting the conclusion that assimilative capacity has declined (Fisher et al. 2000). The decline in K_{net} (Fig. 1A) appears to be slowing in recent years, perhaps indicating that the lake has reached equilibrium under the present state of high external loads. It is unclear whether K_{net} would tend to be higher, lower, or similar to the present value if the lake were to equilibrate under some new lower rate of P loading. We suspect that K_{net} might be higher, in part because of reversal of biological processes described below. However, it is important to note that we presently do not have the information necessary to make a quantitative prediction of these biological effects.

Biological Processes that affect Lake Phosphorus Assimilation

Phosphorus Deficiency vs. Surplus

A major loss process for P from the water column of lakes is the settling of plankton (Stabel 1985). When P is deficient, as is the natural state of many freshwater lakes, very little soluble P remains in the water column and most occurs within the phytoplankton cells, or when there is heavy grazing pressure, in the tissues of zooplankton (Gulati et al. 1992). Under these conditions, the P is contained in particles, which can readily transport it into sediment storage when they settle due to gravity. In contrast, lakes with many years of high P loading can develop a P surplus, where the supply of soluble P exceeds demands of phytoplankton. Under these circumstances some

other factor, such as nitrogen (N) may become "secondarily limiting" (Schelske 1984) and a large portion of the total P occurs in the dissolved form. The net loss of P from the water column is reduced, lowering a lake's K_{net} .

Another process that can affect the net loss of P from a shallow lake's water column is storage of polyphosphates in the algal cells. In Lake Apopka, a Florida lake that is highly enriched with P (Schelske et al. 2000), soluble P generated at the sediment-water interface is stored as polyphosphate by meroplanktonic algae that frequently are resuspended and settle in the water column (Carrick et al. 1993). Paleolimnological data indicate that the amount of settled P as polyphosphate has increased with increased nutrient loading during the last century in this lake (Kenney et al., in review).

In Lake Okeechobee, we do not have comparable data to evaluate the importance of polyphosphate storage, but there is evidence of an increased P surplus in the water column since the early 1970s. In particular, a switch from P-limited to N-limited conditions occurred in the early 1980s (Havens 1995), coincident with an increase in the availability of soluble P relative to soluble N (Smith et al. 1995). In the early 1990s, chemical measurements and nutrient enrichment bioassays (Aldridge 1994) quantified the amount of surplus P for plankton, defined as the sum of hot-water extractable P (Fitzgerald and Nelson 1966) and SRP. It ranged from 20 to 100 mg m⁻³ and represented from 39 to 55% of total P in the water. Although the data for hot-water extractable P are limited to the early 1990s, James et al. (1995b) documented that there was a significant increase in lake-wide SRP concentrations from the early 1970s to the 1990s, and a re-analysis of the current data supports this conclusion (Fig. 1B). The increase coincides with the decline in K_{net} .

Under current conditions, the primary limiting nutrient for pelagic phytoplankton in Lake Okeechobee is N, with P acting only as a co-limiting factor in certain sheltered bays at the south end of the lake (Aldridge et al. 1995). If P loading to this lake is substantially reduced, one might expect these conditions to change, as lowered inputs of P lead to a decreased frequency of N limitation and an increase of P-limited conditions. As the P-limited phytoplankton sequester soluble P, there should be a corresponding reduction in the percent and quantity of P that occurs in that fraction in the water column, and an increased fraction of the total water column P that is susceptible to loss by

sedimentation. That response might be accelerated if there is improvement of underwater irradiance along with lowered phytoplankton biomass, because rates of P uptake by freshwater phytoplankton are directly influenced by light availability (Nalewajko and Lee 1983). Under present conditions, the phytoplankton in Lake Okeechobee often are light-limited due to a combination of abiotic turbidity and a relatively high lake stage. Future management of the lake may include (depending on feasibility) both a lower average lake stage and removal of mud sediment materials that contribute to the high turbidity (USACE 1999). Those actions could be complementary to P load reduction, in terms of improving the water quality of the lake, if they result in greater net P assimilation.

Phytoplankton Community Structure

The taxonomic composition of phytoplankton also may influence the extent to which P is lost from the water column by sedimentation, and hence the ability of a lake to assimilate external P loads. In considering the factors that affect the vertical distribution of phytoplankton in lakes, Reynolds (1984) identifies three general categories of algal cells: (a) non-motile, negatively buoyant; (b) positively buoyant; and (c) neutrally buoyant and motile. Among the negatively buoyant algae, planktonic diatoms are the prime example. Their protoplasts are surrounded by a siliceous frustule, which makes them very dense relative to the fresh water medium. As a result they sink rapidly and only can maintain a net growth in turbulent water (Lund et al. 1963, Reynolds 1973, Reynolds and Wiseman 1982). When the lake water is thermally stratified, diatoms settle to the lake bottom, resulting in a downward flux of P. In contrast, many of the planktonic cyanobacteria are positively buoyant, meaning that they will float, rather than sink, in a stratified water column (Reynolds 1984). By the formation of intra-cellular gas vacuoles (Reynolds and Walsby 1975), many cyanobacteria species can rise to the water surface forming scums or blooms. Cyanobacteria that occur at the sediment-water interface also may remain dormant until favorable conditions of irradiance, temperature, and/or nutrient availability occur, and then migrate upwards in the water column (Horne 1979, Barbiero and Kann 1994). Hence, the relative dominance of negatively buoyant vs. positively buoyant algae in a lake may influence that extent of P transport from the water to sediments (Barbiero and Welch 1992), and therefore determine in part the lake's K_{net} .

Dominance by diatoms would tend to favor a high K_{net} , while dominance by cyanobacteria would contribute to a K_{net} that is relatively low.

In the case of Lake Okeechobee, there has been a dramatic change in phytoplankton taxonomic structure coincident with the observed decrease in K_{net} from the 1970s to the 1990s (Fig. 1C). In a survey conducted in 1974 (Marshall 1977), diatoms comprised 45% of the total phytoplankton biomass in the lake's pelagic (open-water) region, while less than 30% was due to cyanobacteria. The remainder of the biomass was made up of cryptophytes and small chlorophytes, taxa that Reynolds (1994) classifies as neutrally buoyant. In contrast, the phytoplankton community that has dominated in the lake since the late 1980s contains over 60% cyanobacteria and just 20% diatoms (Cichra et al. 1995, Havens et al. 1998). The dominance by cyanobacteria probably is related to the secondary N limitation that now occurs in the lake (Smith et al. 1995, Phlips et al. 1997) and not a lack of silica in these silica-replete waters. The dominant taxa (e.g., *Anabaena circinalis*) are favored over other algae when N is limiting because they can sequester N_2 from the atmosphere when dissolved inorganic N is scarce (Horne 1977). If the rate of P loading is substantially reduced and in-lake P concentrations decline, the frequency of N-limiting conditions may be reduced in Lake Okeechobee. If that occurs, there may be a reversal of the trend in phytoplankton taxonomic structure, with a return to diatom dominance, and perhaps an increase in K_{net} . With a greater K_{net} , the in-lake P concentration goal might be met with a higher TMDL.

Submerged Plant Distribution and Biomass

Highly eutrophic shallow lakes can exist in two distinct states -- clear and turbid (Scheffer 1989, Scheffer et al. 1993). A low biomass of phytoplankton in the water column and widespread dense growth of submerged macrophytes characterize clear water lakes. The macrophytes provide a number of functions related to water quality and P dynamics. These include a stabilization of sediments by roots, a reduction of water flow velocity and shear stress on the sediment surface due to wave attenuation (Vermaat et al. 2000), trapping of sediments among the macrophytes, direct uptake of P by roots in the sediments and direct uptake of P from the water by epiphytic algae (Carrigan and Kalff 1982, Burkholder et al. 1990, Hansson 1990). The net result is that in lakes with strong

macrophyte dominance, there is a positive feedback system that prevents phytoplankton from becoming abundant and maintains a strong in-lake sink for P. In Florida lakes dominated by macrophytes, as much as 96% of the combined water column and macrophyte phosphorus can occur in the tissues of the macrophytes (Canfield et al. 1983). These conditions should contribute to a high K_{net} . In contrast, turbid phytoplankton-dominated lakes generally contain sparse or no submerged macrophytes (Scheffer et al. 1994, Moss et al. 1997), and their sediments are more prone to wind and wave driven sediment resuspension. This alternative condition also generates a positive feedback, because increased phytoplankton \rightarrow greater turbidity \rightarrow insufficient light for submerged macrophytes \rightarrow more nutrients available to phytoplankton \rightarrow more phytoplankton. These lakes are characterized by P-replete conditions and cyanobacterial dominance (Smith 1986, Hosper 1997) and for the reasons listed above, can be expected to have lower values of K_{net} than their clear water counterparts.

In Lake Okeechobee, the central pelagic zone generally has a high degree of turbidity due to resuspension of inorganic bottom sediments, and as a result of the poor light conditions, does not support either rooted macrophytes or a high biomass of phytoplankton (Phlips et al. 1995, Zimba et al. 1995). The shoreline areas of the lake, by contrast, have displayed distinct transitions in the last 20 years between clear water with dense macrophytes and turbid water with dense phytoplankton, similar to what has been observed in some shallow European lakes that have experienced water level fluctuations (Blindow 1992, Meijer 2000). During the latter half of the 1990s, many successive years of high water levels led to a large-scale loss of submerged plant communities, and there was turbid water, high concentrations of P, and phytoplankton blooms (Havens 1997, SFWMD 2000). In contrast, the shoreline area of the lake dramatically switched to a clear water macrophyte-dominated state in summer 2000, coincident with a managed lake recession carried out by the South Florida Water Management District. Shoreline areas that had no macrophytes and over 150 mg m^{-3} total P in April had macrophyte plant beds and less than 20 mg m^{-3} total P in July-September. Although the transition between turbid and clear states appears to be controlled primarily by water depth (Steinman et al. 1997), reduced P loads might help to facilitate macrophyte growth by increasing light availability (less attenuation by phytoplankton) for any given depth regime.

Regardless of the causal mechanism, a high biomass of macrophytes in Lake Okeechobee could contribute to greater P assimilation and allow the lake water to maintain a lower average P concentration at any given rate of external loading.

Invertebrate and Fish Community Structure

The taxonomic composition of benthic invertebrates also can influence the P dynamics of lakes, by processes including feeding / excretion and vertical migration. If migratory invertebrate predators occur at high densities, they may graze a large biomass of plankton in the water column at night (Saunders and Lewis 1988), and then transport this material and its associated P into the sediments during daytime hours. The total quantity of downward P transport will depend on the extent to which consumed P is excreted while the animals still are in the water column and whether fecal material produced in the water column is sedimented. *Chaoborus*, *Chironomus*, and other benthic invertebrates that exit the lake as winged adults at the end of their larval development also may serve to export P from the ecosystem into the watershed. The yearly emergence of chironomids from a shallow lake in Japan accounted for a net loss of 11 metric tons of P, which was more than 10% of the total P loss including outflow from tributaries (Iwakuma 1992, Havens et al. 2000). In contrast, certain benthic invertebrates such as oligochaete worms do not undergo vertical migration or emergence from the lake and do not provide for these loss processes. Instead they may facilitate a large upward flux of dissolved P into the water column as a result of their bioturbation and feeding activities (Van Rees et al. 1996). Oligochaetes consume particulate organic material in the sediments and excrete waste material containing the soluble nutrients into the overlying water. If a lake were to experience a strong transition towards oligochaete dominance, as often occurs during cultural eutrophication (Brinkhurst 1974), one might expect this to contribute to a lower K_{net} .

In addition to the processes described above, certain macro-invertebrate assemblages can remove particulate P from the water column at high rates by filtration activities and this can dramatically affect a shallow lake's P cycle. One of the best examples is the zebra mussel (*Dreissena polymorpha*), which has caused dramatic increases in transparency, reduced phytoplankton biomass, and reduced water column

total P concentrations in shallow regions of the Laurentian Great Lakes (Nalepa and Fahnenstiel 1995, Makarewicz et al. 2000). The primary mechanism responsible for reduced total P is biological storage in mussel biomass, which has a very slow turnover rate compared to that of plankton populations.

Certain fish taxa also are known to strongly affect P cycling, especially in eutrophic shallow lakes (Moss et al. 1997). One of best-studied examples is the gizzard shad (*Dorosoma cepedianum*), a fish that ingests organic detritus in lake sediments and then excretes soluble N and P into the water column. In a shallow lake in Ohio, USA, Schaus et al. (1997) documented that the loading of dissolved P to the water column by shad "exceeded inputs from the relatively large and highly agricultural watershed." The calculated load was greater than diffusive release of P from the anoxic lake sediments. A number of studies have shown that other benthic feeding fish may contribute large quantities of P to the lake's water column (Lamarra 1975, Brabrand et al. 1990, Mather et al. 1995). In lakes with a high percentage of benthivorous fish, one might expect a lower K_{net} than in lakes with fewer of these fish.

In Lake Okeechobee, current conditions of the macro-invertebrates and fish are consistent with high internal P loading and a low value of K_{net} . Warren et al. (1995) reported that oligochaete abundance was near 30% in 1969-1973, but accounted for 80% of total macro-invertebrate abundance by the 1990s (Fig. 1D). Van Rees et al. (1996) quantified the amount of dissolved P loading that could be attributed to these animals, and concluded that it might be 2 to 15 times greater than that caused by diffusive fluxes from the sediments. In Lake Okeechobee the density of the dominant oligochaete species, *Limnodrilus hoffmeisteri*, is typical of highly eutrophic lakes. The increased relative abundance of oligochaetes coincided with (and perhaps contributed to) the decline in observed K_{net} . It is unclear whether the trend in macro-invertebrate community structure will reverse if the lake experiences substantially lower rates of P loading.

There are no long-term data on fish community structure in Lake Okeechobee to allow for a comparison of changes in species dominance with the trend in K_{net} . A comprehensive study performed in the early 1990s, however, does indicate that the lake supports a high biomass of detritivorous fish, including gizzard shad and various types of catfish (Bull et al. 1995). It again is difficult to predict how the fish community might

change under conditions of reduced external P loading in this subtropical system, but studies on temperate lakes suggest that both the total biomass of fish and the relative biomass of detritivores might decline (Persson et al. 1988).

Summary

Geochemical processes at the sediment-water interface (in particular diffusion of soluble P governed by redox potential and iron) may largely determine the equilibrium K_{net} in eutrophic lakes, as well as responses to external P loading. These processes generally are considered in lake water quality models, including one of the models used to establish a proposed TMDL for Lake Okeechobee (Pollman 2000). However, biological processes such as those described above also may play a role, and should be given consideration when quantitative estimates of their impact on P dynamics become available. A complex water quality model for the lake (James et al. 1997) that presently is undergoing re-calibration includes P uptake and settling losses of three distinct algal groups (diatoms, cyanobacteria, and chlorophytes). In the near future this model could be modified to include: (1) the effects of submerged plant macrophyte; (2) a better consideration of the ecosystem's spatial variability (Schelske 1989, Philips et al. 1993); and (3) other biological processes described herein. Recognizing that our understanding of the ecosystem is under development, state and federal agencies have recommended that the lake's TMDL be "revisited" at approximately 5-year intervals. The next iteration of a P loading target for Lake Okeechobee might therefore include explicit consideration of the biological processes described here. If reduced P loading ever does result in a reversal of biological changes that occurred with cultural eutrophication (this might take decades), the ultimate loading target might be greater than presently is proposed. Therefore the iterative TMDL process is critical for management of this lake ecosystem, and it represents a sound approach for dealing with other nutrient-impacted shallow lakes.

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References

Aldridge, F.J., 1994. Application of nutrient enrichment bioassays to evaluate spatial and temporal limiting nutrient patterns and to estimate surplus phosphorus concentrations in Lake Okeechobee, Florida. Doctoral Dissertation, University of Florida, Gainesville, FL.

Aldridge, F.J., Phlips, E.J., Schelske, C.L., 1995, The use of nutrient enrichment bioassays to test for spatial and temporal distribution of limiting factors affecting phytoplankton dynamics in Lake Okeechobee, Florida. Arch. Hydrobiol., Advances in Limnol. 45, 177-190.

Barbiero, R.P., Kann, J., 1994. The importance of benthic recruitment to the population development of *Aphanizomenon flos-aquae* and internal loading in a shallow lake. J. Plankton Res. 16, 1581-1588.

Barbiero, R.P., Welch, E.B., 1992. Contribution of benthic blue-green algal recruitment of lake populations and phosphorus translocation. Freshwater Biol. 27, 249-260.

Blindow, I., 1992. Long and short term dynamics of submerged macrophytes in two shallow lakes. Freshwater Biol. 28, 15-27.

Brabrand, A., Faafeng, B.A., Nilssen, J.P.M., 1990. Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. Can. J. Fish. Aquat. Sci. 47, 364-372.

Brinkhurst, R.C., 1974. The Benthos of Lakes. Macmillan Press, London, UK.

- Bull. L.A., Fox, D.D., Brown, D.W., Davis, L.J., Miller, S.J., Wulfschleger, J.G., 1995. Fish distribution in limnetic areas of Lake Okeechobee, Florida. *Arch. Hydrobiol., Advances in Limnol.* 45, 333-342.
- Burkholder, J.M., Wetzel, R.G., Klomparens, K.L., 1990. Direct comparison of phosphate uptake by adnate and loosely attached microalgae within an intact biofilm matrix. *Appl. Environ. Microbiol.* 56, 2882-2890.
- Canfield, D.E., Jr., Langeland, K.A., Maceina, M.J., Haller, W.T., Shireman, J.V., Jones, J.R., 1983. Trophic classification of lakes with aquatic macrophytes. *Can. J. Fish. Aquat. Sci.* 40, 1713-1718.
- Carrick, H.J., Aldridge, F.J., Schelske, C.L., 1993. Wind influences phytoplankton biomass and composition in a shallow productive lake. *Limnol. Oceanogr.* 38, 1179-1192.
- Carrigan, R., Kalff, J., 1982. Phosphorus release by submerged macrophytes: significance to epiphyton and phytoplankton. *Limnol. Oceanogr.* 27, 419-427.
- Cichra, M.F., Badylak, S., Henderson, N, Rueter, B.H., Philips, E.J., 1995. Phytoplankton community structure in the open water zone of a shallow subtropical lake (Lake Okeechobee, Florida, USA). *Arch. Hydrobiol., Advances in Limnology* 45, 157-175.
- Cullen, P., Forsberg, C., 1988. Experiences with reducing point sources of phosphorus to lakes. *Hydrobiologia* 170, 321-336.
- Fisher, M.M, Reddy, K.R., James, R.T., 2000. Long-term changes in the sediment chemistry of a large shallow subtropical lake. *Lake Reserv. Manage.*, in review.
- Fitzgerald, G.P., Nelson, T.C., 1966. Extractive and enzymatic analysis for limiting or surplus phosphorus in algae. *J. Phycol.* 2, 32-37.

Gulati, R.D., Ooms-Wilms, A.L., Van Tongeren, O.F.R., Postema, G., Siewertsen, K., 1992. The dynamics and role of limnetic zooplankton in the Loosdrecht lakes (The Netherlands). *Hydrobiologia* 233, 69-86.

Hansson, L.A., 1990. Quantifying the impact of periphytic algae on nutrient availability for phytoplankton. *Freshwater Biol.* 24, 265-273.

Havens, K.E., 1995. Secondary nitrogen limitation in a subtropical lake impacted by non-point source agricultural pollution. *Environ. Pollut.* 89, 241-246.

Havens, K.E., 1997. Water levels and total phosphorus in Lake Okeechobee. *Lake Reserv. Manage.* 13, 16-25.

Havens, K.E., Aumen, N.G., James, R.T., Smith, V.H., 1996. Rapid ecological changes in a large subtropical lake undergoing cultural eutrophication. *Ambio* 25, 150-155.

Havens, K.E., Fukushima, T., Xie, P., Iwakuma, T., James, R.T., Takamura, N., Hanazato, T., Yamamoto, T., 2000. Nutrient dynamics and the eutrophication of shallow lakes Kasumigaura (Japan), Donghu (P.R. China), and Okeechobee (USA). *Environ. Pollut.*, in press.

Havens, K.E., Philips, E.J., Cichra, M.F., B.L. Li., 1998. Light availability as a possible regulator of cyanobacteria species composition in a shallow subtropical lake. *Freshwater Biol.* 39, 547-556.

Havens, K.E., Steinman, A.D., 1995. Aquatic systems. In: Reheigl, J.E. (Ed.), *Soil Amendments: Impacts on Biotic Systems*, pp. 121-151. CRC Press, Boca Raton, Florida, USA.

Hecky, R.E., Kilham, P., 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* 33, 796-822.

Horne, A.J., 1977. Nitrogen fixation - a review of this phenomenon as a polluting process. *Prog. Wat. Tech.* 8, 359-372.

Horne, A.J. 1979. Nitrogen fixation in Clear Lake, California. Diel studies on *Aphanizomenon* and *Anabaena* blooms. *Limnol. Oceanogr.* 24, 329-241.

Hosper, H., 1997. Clearing Lakes: An Ecosystem Approach to the Restoration and Management of Shallow Lakes in The Netherlands. Ministry of Transport, Public Works and Water Management, Lelystad, the Netherlands.

Iwakuma, T., 1992. Emergence of Chironomidae from the shallow eutrophic Lake Kasumigaura, Japan. *Hydrobiologia* 245, 27-40.

James, R.T., Jones, B.L., Smith, V.H., 1995a. Historical trends in the Lake Okeechobee ecosystem II. Nutrient budgets. *Arch. Hydrobiol. Suppl.* 107, 25-47.

James, R.T., Martin, J., Wool, T., Wang, P.F., 1997. A sediment resuspension and water quality model of Lake Okeechobee. *J. Am. Water Res. Assoc.* 33, 661-680.

James, R.T., Smith, V.H., Jones, B.L., 1995b. Historical trends in the Lake Okeechobee ecosystem III. Water quality. *Arch. Hydrobiol. Suppl.* 107, 49-69.

Kenny, W.F., Schelske, C.L., Chapman, A., (in review). Polyphosphate sedimentation in a hypereutrophic lake: implications for modeling, management and paleolimnology.

Lamarra, V.A., Jr., 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. *Verh. Int. Ver. Limnol.* 19, 2461-2468.

Lund, J.W.G., Mackereth, F.J.H., Mortimer, C.H., 1963. Changes in depth and time of certain chemical and physical conditions and of the standing crop of *Asterionella formosa* Hass. in the north basin of Windermere in 1947. Phil. Trans. Royal Soc. London B 246, 255-290.

Makarewicz, J.C., Bertram, P., Lewis, T.W., 2000. Chemistry of the offshore surface waters of Lake Erie: pre- and post-*Dreissena* introduction (1983-1993). J. Great Lakes Res. 26, 82-93.

Marshall, M.L., 1977. Phytoplankton and primary productivity studies in Lake Okeechobee during 1974. South Florida Water Management District Technical Publication 77-2, West Palm Beach, Florida, USA.

Mather, M.A., Vanni, M.J., Wissing, T.E., Davis, S.A., Schaus, M.H., 1995. Regeneration of nitrogen and phosphorus by bluegill and gizzard shad: effect of feeding history. Can. J. Fish. Aquat. Sci. 52, 2327-2338.

Meijer, M.L., 2000. Biomanipulation in The Netherlands - 15 Years of Experience. Ministry of Transport, Public Works and Water Management, Lelystad, The Netherlands.

Moss, B., Madgwick, J., Phillips, G., 1997. A Guide to the Restoration of Nutrient-Enriched Shallow Lakes. Environment Agency, Broads Authority, UK.

Nalepa, T.F., Fahnenstiel, G.L., 1995. *Dreissena polymorpha* in the Saginaw Bay, Lake Huron ecosystem: overview and perspective. J. Great Lakes Res. 21, 411-416.

Nalewajko, C., Lee, K., 1983. Light stimulation of phosphate uptake in marine phytoplankton. Mar. Biol. 74, 9-15.

Paerl, H.W., 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol. Oceanogr.* 33, 823-847.

Persson, L., Andersson, G., Hamrin, S.F., Johansson, L., 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In: Carpenter, S.R. (Ed.), *Complex Interactions in Lake Communities*, pp. 45-65. Springer-Verlag, New York.

Phlips, E.J., Aldridge, F.J., Hansen, P., 1995. Patterns of water chemistry, physical and biological parameters in a shallow subtropical lake (Lake Okeechobee, Florida, USA). *Arch. Hydrobiol., Advances in Limnol.* 45, 117-135.

Phlips, E.J., Cichra, M., Havens, K.E., Hanlon, C., Badylak, S., Rueter, B., Randall, M., Hansen, P., 1997. Relationships between phytoplankton dynamics and the availability of light and nutrients in a shallow subtropical lake. *J. Plankton Res.* 19, 319-342.

Pollman, C., 2000. Phosphorus transport model for Lake Okeechobee - major model revisions. Technical document prepared for the Lake Okeechobee TMDL Technical Advisory Committee. Florida Department of Environmental Protection, Tallahassee, Florida, USA.

Reynolds, C.S., 1973. The seasonal periodicity of planktonic diatoms in a shallow eutrophic lake. *Freshwater Biol.* 3, 89-110.

Reynolds, C.S., 1978. Phosphorus and the eutrophication of lakes - a personal view. *Ciba Foundation Symposium* 57, 201-228.

Reynolds, C.S., 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, UK.

Reynolds, C.S., Walsby, A.E., 1975. Water blooms. *Biol. Rev. Cambridge Phil. Soc.* 50, 437-481.

Reynolds, C.S., Wiseman, S.W., 1982. Sinking losses of phytoplankton in closed limnetic systems. *J. Plankton Res.* 4, 489-522.

Saunders, J.R., Lewis, W.M., Jr., 1988. Dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). *Ecol. Monogr.* 58, 337-353.

Schaus. M.H., Vanni. M.J., Wissing, T.E., Bremigan, M.T., Garvey, J.E., Stein, R.A. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnol. Oceanogr.* 42, 1386-1397.

Scheffer, M., 1989. Alternative stable states in eutrophic shallow freshwater systems: a minimal model. *Hydrobiol. Bull.* 23, 73-85.

Scheffer, M., 1998. *Ecology of Shallow Lakes*. Chapman and Hall, London, UK.

Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends in Ecol. and Evol.* 8, 275-279.

Scheffer, M. Van den Berg, M. Breukelaar, A., Breukers, C., Coops, H., Doef, R., Meijer, M.L., 1994. Vegetated areas with clear water in turbid shallow lakes. *Aquat. Bot.* 49, 193-196.

Schelske, C.L., 1984. In situ and natural phytoplankton assemblage bioassays. In: Shubert, L.E. (Ed.), *Algae as Ecological Indicators*, pp. 15-47. Academic Press, NY.

Schelske, C.L., 1989. Assessment of nutrient effects and nutrient limitation in Lake Okeechobee. *Water Res. Bull.* 25, 1119-1130.

Schelske, C.L., Aldridge, F.J., Kenny, W.F., Cable, J.E., 2000. Wind or nutrients: historic development of hypereutrophy in Lake Apopka, Florida: limnology and lake management. *Arch. Hydrobiol., Advances in Limnol.* 55, 543-563.

Schindler, D.W., 1977. Evolution of phosphorus limitation in lakes. *Science* 195, 260-262.

SFWMD. 2000. Surface water improvement and management (SWIM) plan for Lake Okeechobee, update. South Florida Water Management District, Florida, USA.

Smith, V.H., 1986. Light and nutrient effects on the relative biomass of blue-green algae in lake phytoplankton. *Can. J. Fish. Aquat. Sci.* 43, 148-153.

Smith, V.H., Bierman, V.J., Jones, B.L., Havens, K.E., 1995. Historical trends in the Lake Okeechobee ecosystem IV. Nitrogen:phosphorus ratios, cyanobacterial nitrogen fixation, and nitrogen fixation potential. *Arch. Hydrobiol. Suppl.* 107, 71-88.

Smith, V.H., Tilman, G.D., Nekola, J.C., 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* 100, 179-196.

Stabel, H.H., 1985, Mechanisms controlling the sedimentation of various elements in prealpine lakes. In: Stumm, W. (Ed.), *Chemical Processes in Lakes*, pp. 143-167. John Wiley & Sons, New York, USA.

Steinman, A.D., Meeker, R.H., Rodusky, A.J., Davis, W.P., Hwang, S.J., 1997. Ecological properties of charophytes in a large subtropical lake. *J. N. Am. Benthol. Soc.* 16, 781-793.

USACE. 1999. Central and Southern Florida Project comprehensive review study. Final integrated feasibility report and programmatic environmental impact statement. US Army Corps of Engineers, Jacksonville, Florida, USA.

Van Rees, K.C.J., Reddy, K.R., Rao, P.S.C., 1996. Influence of benthic organisms on solute transport in lake sediments. *Hydrobiologia* 317, 31-40.

Vermaat, J.E., Santamaria, L., Roos, P.J., 2000. Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. *Arch. Hydrobiol.* 148, 549-562.

Vollenweider, R.A. 1975, Input-output models with special reference to the phosphorus loading concept in limnology. *Schweiz. Zeit. Hydrol.* 37, 53-84.

Walker, W.W., Jr., 2000. Revised TMDL calculations - refinements to steady-state model. Technical document prepared for Lake Okeechobee TMDL Technical Advisory Committee. Florida Department of Environmental Protection, Tallahassee, Florida, USA.

Warren, G.L., Vogel, M.J., Fox, D.D., 1995. Trophic and distributional dynamics of Lake Okeechobee sublittoral benthic invertebrate communities. *Arch. Hydrobiol., Advances in Limnology* 45, 317-332.

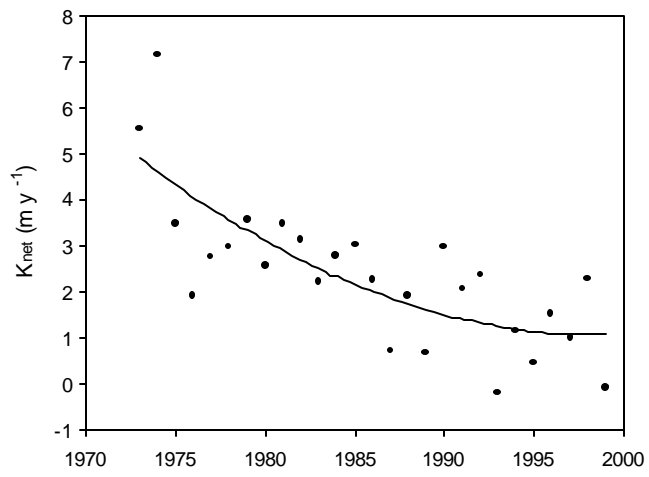
Zimba, P.V., Hopson, M.S., Smith, J.P., Colle, D.E., Shireman, J.V., 1995. Chemical composition and distribution of submersed aquatic vegetation in Lake Okeechobee, Florida (1989-1991). *Arch. Hydrobiol., Advances in Limnol.* 45, 241-246.

Table 1. Biological factors that may influence a lake's net phosphorus (P) assimilative capacity, which we index in this paper as K_{net} , the net P settling rate.

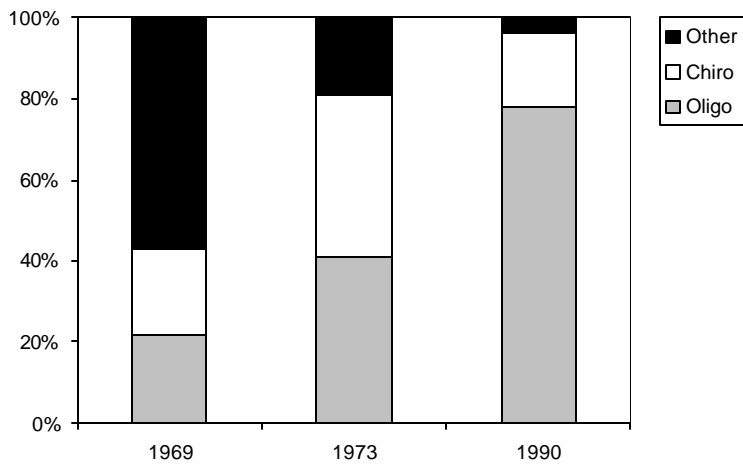
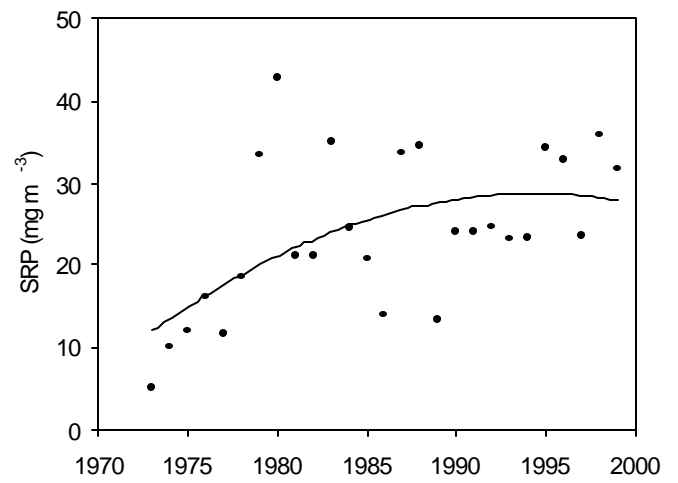
Biological Factor	Effect on K_{net}	Response to Load Reduction
Phosphorus surplus	Reduced when surplus is great	Surplus should be reduced if loads are reduced = increased K_{net}
Phytoplankton taxonomic structure	Highest when diatoms are dominant; lowest when buoyant cyanobacteria are dominant	Relative biomass of cyanobacteria expected to decrease if loads are reduced and P becomes limiting = increased K_{net}
Submerged plant biomass	Highest when there is widespread high biomass of plants	Unclear whether this factor is affected by nutrient inputs per se or primarily by water depths = uncertain effect on K_{net}
Macro-invertebrate taxonomic structure & biomass	Highest when vertically migrating insects dominate with adult emergence from the lake; lowest with oligochaete dominance	Relative biomass of oligochaetes expected to decrease if loads are substantially reduced = increased K_{net}
Fish taxonomic structure & biomass	Highest when detritivores are not abundant; lowest when the biomass of these fish (especially gizzard shad) is very high	Reduced total fish biomass and decreased relative biomass of detritivores = increased K_{net}

Fig. 1. Chemical and biological changes in Lake Okeechobee in the last 30 years. A. Exponential decline in K_{net} , the net phosphorus settling rate calculated from mass-balance. B. Increase in yearly-averaged soluble reactive phosphorus (SRP) concentrations measured at eight pelagic monitoring stations. C. Changes in the relative abundance of different benthic invertebrate taxa, including chironomids (Chiro) and oligochaetes (Oligo). C. Changes in the relative biovolume of different phytoplankton taxa, including diatoms, chlorophytes (Chloro) and cyanobacteria (Cyano).

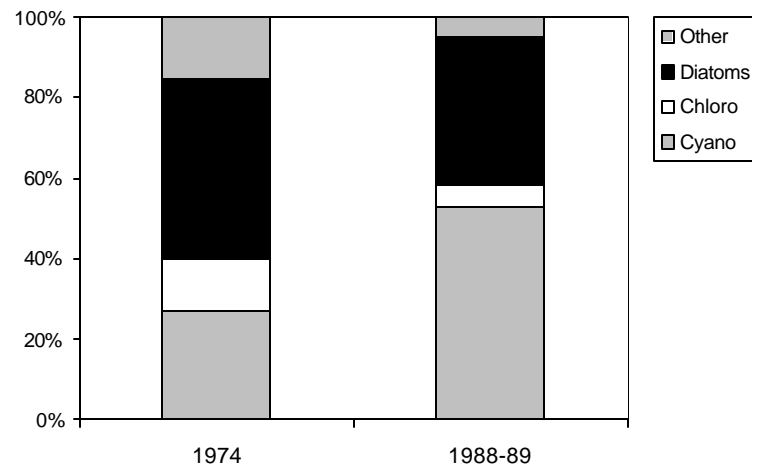
A



B



C



D